Effects of Spatial Network Structure on Competitive Coexistence in a Metacommunity

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Abstract

Species dispersal patterns are often assumed to take place on a uniform environment and do not allow species to move through a habitat without effecting the dynamics locally. We examine the effects of migration network topology on a the outcome of competitive interactions between two competing species which may disperse non-uniformly and are allowed to jump between habitats without effecting the populations between. We develop a perturbation model for a fully-connected migration network and apply this approximate model to networks with highly clustered subsets. We show that highly clustered networks allow for the coexistence of competitors and that these coexistence states disappear quickly when the highly clustered networks are randomly rewired. Moreover, we examine the effect of migration network topology on the colonization of habitat by an invasive species and show the relation between this problem and our previous results.

Introduction

The first mathematical model of competing species was proposed by Lotka (1925) and Volterra (1926) and since their pioneering work the question of coexistence between competing species has occupied a central theme in ecology. In the case of two competing species the Lotka-Volterra model led to the formulation of the competitive exclusion principle, which states that two species in direct competition cannot coexist. However, while the exclusion principle has been observed experimentally in a number of cases ([5] [7], [6], [8]) there is an ever growing list of cases where it appears to be violated ([11]). Given the simplicity of the model the existence of exceptions is hardly surprising, however the task remains to identify which of the assumptions underlying the model are violated in these cases. The lack of a spatial dimension in the original Lotka-Volterra model is one assumption that is clearly violated in nature and the introduction of a spatial dimension does not alter the assumptions about the nature of the competitive interaction between the species. Therefore, spatial effects on the outcome of species competitive interactions have garnered a large amount of attention in the literature ([9], [3]).

Metapopulation models treat the landscape as a network of suitable habitat patches ([4]). The environment is assumed to be divided up into a collection of well-mixed populations which are connected by comparatively rare migration events. For many species like amphibians this is the appropriate model for their dispersal and colonization dynamics where each habitat patch is a pond([3]). Furthermore, we expect this approximation to be valid for any species whose dispersal operates on two distinct scales of well-mixed interactions within a local population and comparatively rare long distance dispersal. Previous work has demonstrated validity of approximating landscape connectivity by a complex network ([10], [1]).

A typical assumption is that the connections between these populations form a two dimensional lattice in which populations close to one another geographically are connected ([9], [2]). However, this topology assumes species move between habitats in step-wise manner and does not allow species to jump to a new habitat without first moving though and effecting the dynamics of the habitat between the two endpoints. Clearly, this regularity in the connections between habitats is not always the case. For instance, in a population of wind-dispersed plants a population on the top of a hill may have many more habitats which it may disperse to in comparison to a valley population. Bird dispersal patterns provide another example where species may move through habitats without affecting the dynamics. In general, geographical obstacles and a lack of convexity in species dispersal patterns may confound the simple lattice topology and lead a more interesting and complex topology for the network of connections between habitats. By studying the effects of graph topology on the outcome of a two-species competition we may better understand the spatial effects for discrete populations and well as compare the relative merits of different types of spatial heterogeneity in terms of preserving biodiversity.

In this work we investigate the role of the network topology in species coexistence with an emphasis on "barbell" type networks–networks with highly connected subnetworks with relatively few connections between the highly connected clusters. These networks provide an especially appealing case for theoretical work because they can be largely understood by their relation to a fully

connected network. Therefore, we begin my developing an approximate perturbation model for the behavior of a fully connected network and apply this reasoning to more complex network topologies. Moreover, we also investigate the importance of network topology to the invasion problem for two competing species. An understanding of the effects of the network topology and the sensitivity of the system to changes in the network topology are important to understand from a conservation standpoint due to the effect of human activity on shaping the topology of migration networks.

The Model

The Lotka-Volterra equations for two-species competing on a network of populations can be modeled as,

$$\begin{array}{l} \frac{dN_1^i}{dt} = rN_1^i(1 - \frac{N_1^i}{K} - c_1N_2^i) + D\sum_{j=1}^{M} A_{ij}(N_1^j - N_1^i) \\ \frac{dN_2^i}{dt} = rN_2^i(1 - \frac{N_2^i}{K} - c_2N_1^i) + D\sum_{j=1}^{M} A_{ij}(N_2^j - N_2^i), \end{array} \tag{1}$$

where $N_{1,2}^i$ represent the populations of each species (1,2) at node i. For simplicity assume that each species has the same growth rate r and the same carrying capacity K. Furthermore, we assume that each species that the rate of dispersal D from a population is uniform and is evenly divided between each of the M connections. Also, we assume both species are equal competitors $c_1 = c_2$. Thus, we concentrate on the effect of the network topology defined by the matrix A_{ij}. A_{ij} is a symmetric matrix whose rows and columns sum are normalized to sum to one. Put into nondimensional form the equations become,

$$\begin{array}{ll} \frac{du^i}{d\tau} = u^i(1 - u^i - c_1v^i) + \rho\sum_{j=1}^{M} A_{ij}(u^j - u^i) & \\ \frac{dv^i}{d\tau} = v^i(1 - v^i - c_2v^i) + \rho\sum_{j=1}^{M} A_{ij}(u^j - u^i) & \\ u^i = \frac{N_1^i}{K} & v^i = \frac{N_2^i}{K} \\ \tau = rt & \rho = \frac{D}{r}. \end{array} \tag{2}$$

We can interpret the ρ parameter as the fraction of the population which disperses each generation. We are concerned with the limit where ρ can be considered a small parameter for every node in the network. In the limit as $\rho \to 0$ we expect that the local dynamics of the nodes will dominate. That is each node will behave similar to the uncoupled model. Similarly we expect for values of ρ near one the system behavior will be similar to that of a non-spatial model. Therefore, we are concerned species interactions with intermediate dispersal rates where the behavior on both the local and network scale contributes to the dynamics.

Results

Fully Connected Network

Before considering the effect of network topology on the outcome of spatial competition it is useful to consider a fully connected network with N nodes. For a network of this type the equations governing the dynamics at each node are identical, so it provides the simplest case to work with in an analytical

setting. This case also can be used as an approximation for highly connected clusters in a more complex network topology. The equation for the dynamics at any node i in the network is given by,

$$\begin{array}{l} \frac{du_i}{dt} = u_i(1 - u_i - cv_i) + \frac{\rho}{N}\sum_{j=1}^{N} \hat{A}_{ij}(u_j - u_i) \\ \frac{dv_i}{dt} = v_i(1 - v_i - cu_i) + \frac{\rho}{N}\sum_{j=1}^{N} \hat{A}_{ij}(v_j - v_i), \end{array} \tag{3}$$

where the $\frac{1}{N}$ factor has been pulled out of the A_{ij} matrix. To simplify the notation in what follows let $\hat{\rho} = \frac{\rho}{N}$.

Now assume $\hat{\rho}$ is a small parameter. Therefore, let

$$\begin{array}{l} u_j(t) = u_j^0(t) + \hat{\rho}u_j^1(t) + \hat{\rho}^2 u_j^2(t) + ... \\ v_j(t) = v_j^0(t) + \hat{\rho}v_j^1(t) + \hat{\rho}^2 v_j^2(t) + ... \end{array} \tag{4}$$

be an expansion in $\hat{\rho}$ for all of the neighboring nodes. If we assume the initial conditions are given as $[u_j(0), v_j(0)) = (1, 0)$ or $(u_j(0), v_j(0)) = (0, 1)]$ then the dynamics of the zeroth order system are trivial and to zeroth order in $\hat{\rho}$ the system will remain at the fixed point. An expansion gives the following equations for the terms of order one in $\hat{\rho}$,

$$\begin{array}{l} \frac{du_j^1}{dt} = u_j^1 - 2u_j^1u_j^0 - cu_j^1v_j^0 - cu_j^0v_j^1 + \sum_{k=1}^{N}(u_k^0 - u_j^0) \\ \frac{dv_j^1}{dt} = v_j^1 - 2v_j^1v_j^0 - cv_j^1u_j^0 - cv_j^0u_j^1 + \sum_{k=1}^{N}(v_k^0 - v_j^0) \end{array} \tag{5}$$

Now we split the system into the two initial condition cases cooresponding to one species being at fixation at node j, $(u_j(0) = 1, v_j(0) = 0)$ or $(u_j(0) = 0, v_j(0) = 1)$. First consider the case that $u_j(0) = 1$ and $v_j(0) = 0$, then the first order equations in $\hat{\rho}$ simplify to,

$$\begin{array}{l} \frac{du_j^1}{dt} = -u_j^1 - cv_j^1 - (N - \Theta) \\ \frac{dv_j^1}{dt} = (1 - c)v_j^1 + (N - \Theta) \end{array} \tag{6}$$

where Θ is defined to be the number of nodes in the network with initial condition $u(0) = 1, v(0) = 0$. The equation for $v_j^1(t)$ is decoupled and linear and thus can be solved analytically,

$$v_j^1(t) = \frac{N - \Theta}{c - 1}(1 - e^{(1-c)t}). \tag{7}$$

Therefore, we can solve the equation for $u_j^1(t)$ using this solution to find that,

$$u_j^1(t) = \frac{-c(N - \Theta)}{c - 1} - (N - \Theta) + Ae^{-t}. \tag{8}$$

where A is a constant term. The other case where the initial conditions for the node are $u_j^0(t) = 0$ and $v_j^0(0) = 1$ can be worked out in a manner exactly analogous to the first case. In this case, the first order terms satisfy,

$$u_j^1(t) = \frac{\Theta}{c - 1} + A_1e^{-t} \tag{9}$$

and

$$v_j^1(t) = \frac{-c\Theta}{c - 1} - \Theta + A_2e^{-t}. \tag{10}$$

Now consider the node i. We have constructed a two-term perturbative expansion in $\hat{\rho}$ for its neighbors. That is we have the following approximate equations for the dynamics of node i,

$$\begin{array}{l} \frac{du_i}{dt} = (1-\hat{\rho}N)u_i - (u_i)^2 - cu_iv_i + \hat{\rho}\sum_{j=1}^{N}(u_j^0(t) + \hat{\rho}u_j^1(t)) \\ \frac{dv_i}{dt} = (1-\hat{\rho}N)v_i - (v_i)^2 - cv_iu_i + \hat{\rho}\sum_{j=1}^{N}(v_j^0(t) + \hat{\rho}v_j^1(t)). \end{array} \tag{11}$$

Using the calculated values for $u_j^0, u_j^1, v_j^0, v_j^1$ and simplifying the expressions (for u we have the sum equal to $\hat{\rho}\Theta$ (Case I) plus $\hat{\rho}(N-\Theta)$ (Case 2). Performing the simplifications we arrive at the following approximate formulas for u_i and v_i,

$$\begin{array}{l} \frac{du_i}{dt} = (1-\rho)u_i - (u_i)^2 - cu_iv_i + \frac{\rho}{N}\Theta + \frac{2\rho^2}{N^2}(\Theta^2 - \Theta N) + De^{-t} \\ \frac{dv_i}{dt} = (1-\rho)v_i - (v_i)^2 - cv_iu_i + \frac{\rho}{N}(N-\Theta) + \frac{2\rho^2}{N^2}(\Theta^2 - \Theta N) + Fe^{-t} \end{array} \tag{12}$$

where F and D are constants. These exponentially decaying terms De^{-t} and Fe^{-t} do not effect the long term dynamics of the system at node i. Therefore, since we are interested only in the asymptotic behavior of the system and not the transients they may be disregarded from the fixed point and stability analysis. The qualitative behavior of the system is controlled by the two constant expansion terms corresponding to the migration into the node. These constant expansion terms provide the influence of the global state of the network on the dynamics at node i. If we define $\phi = \frac{\Theta}{N}$ then these terms simplify to,

$$\begin{array}{l} M_u(\rho,\phi) = \rho\phi + 2\rho^2(\phi^2 - \phi) \\ M_v(\rho,\phi) = \rho(1-\phi) + 2\rho^2(\phi^2 - \phi). \end{array} \tag{13}$$

The value of the M_u and M_v and therefore the ρ and ϕ parameters determine the nature of the dynamics at node i. At a fixed ϕ value as the value of ρ is increased the system undergoes a saddle-node bifurcation and the system is globally attracted to a fixed point corresponding to exclusion of one species (Figure (1)). As expected when ρ is made sufficiently small both the u and v species have attracting basins. Therefore, for small migration rates the local dynamics dominate the network level dynamics of the system. However, as the value of ρ is allowed to increase the system approaches a limit where the outcome of the node is determined by the value of ϕ; if $\phi > \frac{1}{2}$ then species u will control the node. Thus as ρ increases the global dynamics of the population on the network exhibit an exclusion principle on the whole network scale as opposed to at each node individually.

In the case that the underlying network shows heterogeneity the bifurcations would occur at different parameter values for different nodes in the network. Intuitively, this is because in more complex topologies each neighboring node may have different ϕ_j values which makes an analytical solution intractable. However, we expect that the above should be a useful approximation for barbell networks which contain highly connected subclusters with few connections between those clusters.

Emergence of Communities in a Clustered Network

The intuition gained by the perturbative analysis of the fully connected network can be applied to more ecologically interesting network topologies in order to

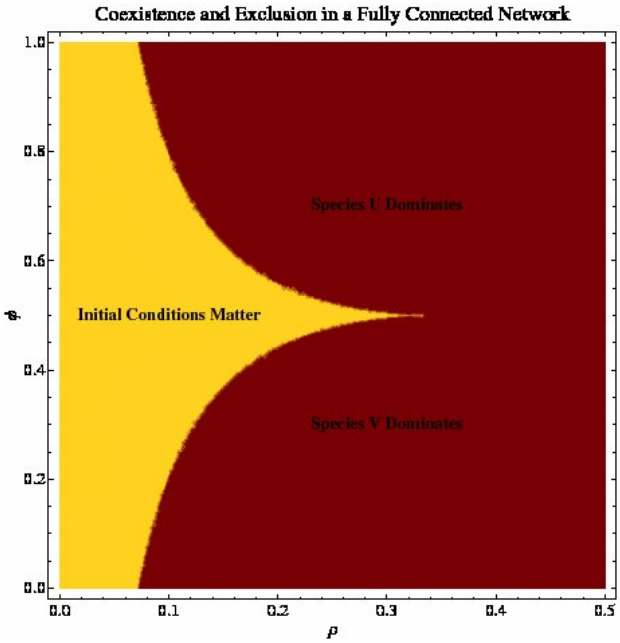

Figure 1: The parameter regions where global and local effects dominate the perturbed model. As the value migration parameter ρ is increased the regions where the steady state at node i is determined by the state of the rest of the network emerge.

understand the emergence of stable multi-node communities within a network. The simplest such extension is for a barbell type network as shown in Figure (2). In this case our analysis of the fully-connected network can be applied approximately to each of the fully connected clusters within the network. In particular, the results for the fully-connected network suggest that each of the fully connected components should act something like individual nodes as the value of ρ is increased. This prediction is easily verified numerically as is shown in Figure (2), where we see that each of the highly connected clusters obeys the exclusion principle approximately but the the network as a whole allows for coexistence.

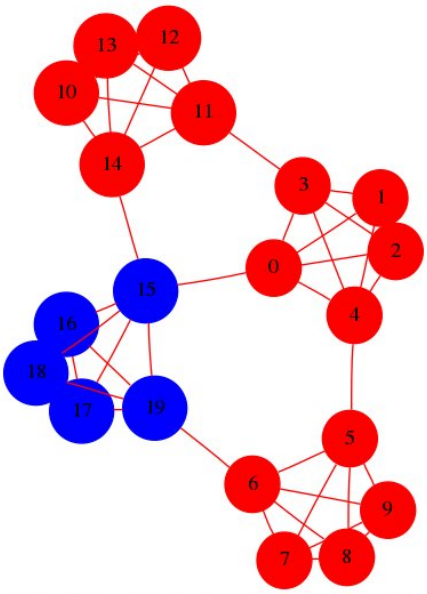

Figure 2: A sample equilibrium for the barbell type network considered here. Red nodes are controlled by species u and blue nodes by species v.

To explore the relationship between the highly connected clusters in the network and coexistence of the global scale on the network we examined how the probability of random initial conditions leading to a coexistence solution depends on this barbell type network structure. To do so we perturbed the barbell type network by randomly rewiring some of the connections in the network while not disconnecting components of the network. The results of these simulations are shown in figure(3) as the number of random rewirings is allowed to vary from zero to twenty-five percent of the total connections. The results show a monotonic decrease in the probability of coexistence as the number of random rewirings is allowed to increase. Moreover, observe that networks closer to the barbell type network probability of coexistence falls off more slowly as the migration term is increased.

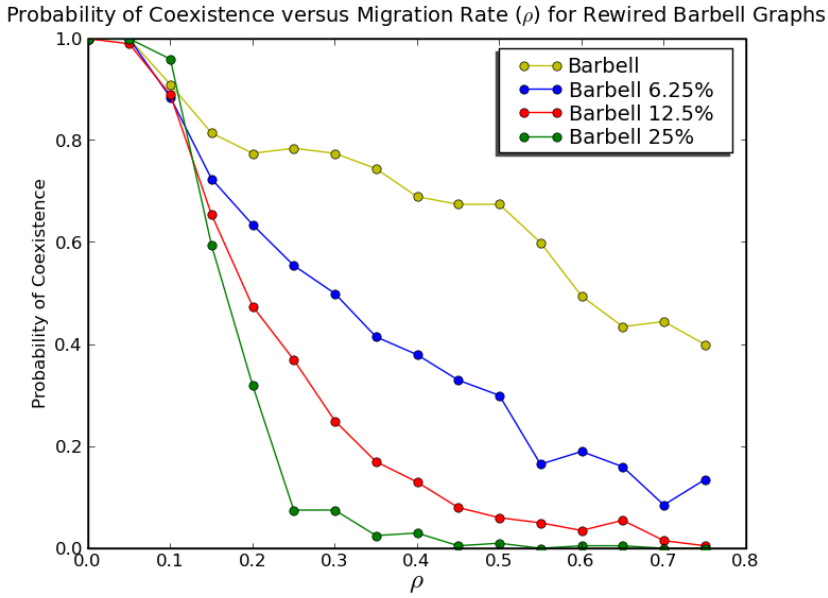

Figure 3: The probability of coexistence for barbell type networks as the value of the migration parameter ρ is increased. The probability of coexistence was estimated by random sample of 80 networks of the given topology with 200 different randomly chosen initial conditions. The competition coefficient is set to $c = 2.0$ and the notation Barbell 6.25% indicates the barbell graph with 6.25% of its connections randomly rewired.

Numerical Topological Results: Invasion Problem

This network framework also lends itself to an examination of the invasibility of different network topologies. In this scenario one species is assumed to represent a native species and occupy every node in the network. The second species can be thought of as a exotic invading species is introduced a k randomly chosen nodes in the network. In this scenario we examined how the network topology effects how many invasion events are required on average for the invading species to establish a stable population.

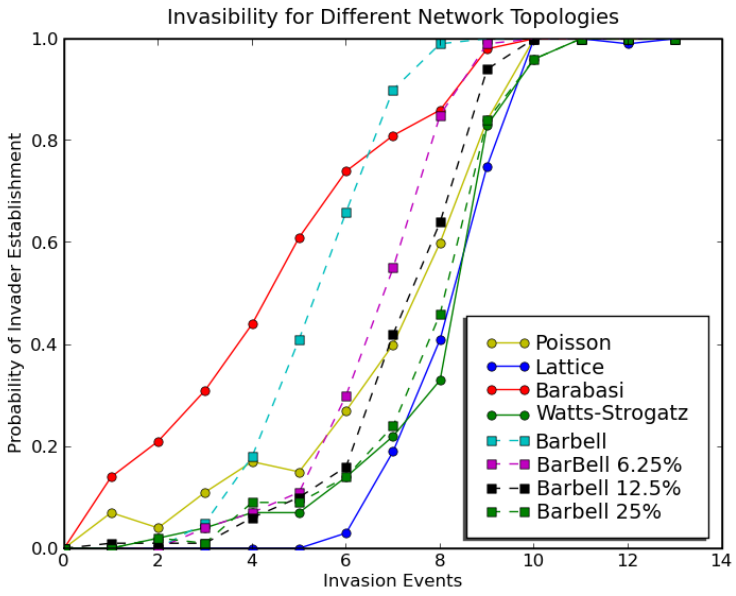

Figure 4: The probability of a successful invasion was estimated by simulating the dynamics of a random perturbation for one hundred networks with each topology. Each curve has $\rho = 0.3$ in this plot.

As before we consider barbell type graphs along with random rewirings of barbell type graphs. Moreover, we also consider a scale-free, small-world, lattice and binomial network types. A binomial or Poisson network topology is characterized by the majority of the nodes having near the mean amount of connections. In contrast, a scale-free network topology is characterized by the existence of "hub" nodes in the network with many more connections than average. A small-world network is characterized by having a short path-length between any two nodes in the network. The barbell type graph and small mutations of it are seen to be the most easily invaded network topologies. The scale-free, small world and binomial network topologies all behave similarly and all of them are more robust to random invasions. The lattice topology provides an intermediate case between the pure barbell network and its most mutated forms.

This trend fits in with our results on coexistence in the networks. A network topology which promotes coexistence solutions necessarily feature one or more

stable fixed points which allow for both species to persist with stable populations. Thus, the basin of attraction leading to coexistence in these networks will in general be larger, meaning a smaller perturbation (invasion) event will be needed to arrive at a fixed point which allows the invading species to establish a stable population. Therefore, network topologies which allow for biodiversity are also more vulnerable to invasion by new competitors.

Discussion

The topology of the migration network which connects suitable habitat patches in an environment can have significant effects on the outcome of two competing species. A fully connected network provides a simple case which can be dealt with in an analytical setting. By using a perturbative analysis we have shown that the behavior of a fully connected network approaches the behavior of the non-spatial model as the migration rate between populations is increased. Thus, an introduction of a spatial dimension is not sufficient in itself to guarantee deviation from the exclusion principle.

However, if a collection of fully connected networks are joined by a few connections the network behavior is significantly different and allows for coexistence of the competing species within each highly connected cluster at higher values of the migration rate. Moreover, this property of barbell networks is seen to decay quickly when the connections are randomly rewired. Moreover, we have demonstrated that highly clustered networks while capable of maintaining biodiversity are also more vulnerable to biological invasions than other common network topologies.

These results suggest that altering even a small fraction of the migration corridors may drastically effect the stability of a competitive interaction in nature. Moreover, this suggests that the individual behavior of the competing species can have a large effect on the outcome of competitive interactions. Indeed, these results suggest that the spatial structuring of the environment introduced by geographical or behavioral biases in the dispersal of the competing species may be vital to coexistence of the competitors. Therefore, from a conservation standpoint it is important to understand the types of network topologies found in natural populations and how human interaction will effect the network topology.

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